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LIII.—*On the Protection of Pollen from Premature Dislodgment or Moisture.* By M. A. Kerner.*

The works of Darwin, Delpino, Hildebrandt, &c., on the part played by insects in the fecundation of phanerogamous plants have lately attracted attention to this subject, and led to numerous observations on the peculiarities of the organization of flowers. The investigation just published by M. Kerner relates to a point which had scarcely been touched previously, but the importance of which can hardly be doubted—namely, the precautions taken to keep the pollen intact until the moment when it is gathered by insects, and especially to preserve it from premature dispersion by means of the wind, or from irremediable injury by water.

There is a large category of plants which escape the dangers just referred to, and the whole organization of which is directed to utilize the action of the wind for the dispersion of pollen. These are the *anemophilous* plants of Delpino, the dry and pulverulent pollen of which escapes in clouds at the least shake. Various peculiarities of organization all accord with the final object to be attained. Thus the flowers, in order to give free access to the wind, are never concealed under leaves, but always suspended at the extremity of slender branches (amentaceous trees), or at the summit of an elevated stalk (grasses, Cyperaceæ, &c.). Moreover, as they have not to

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attract insects, they are generally not remarkable either for colour or perfume; their perianth is generally yellowish or greenish and often scaly; the stamens, instead of being hidden at the bottom of a corolla, are attached to movable catkins, or they push themselves (as in the grasses) above the floral envelope.

In every way a considerable quantity of pollen is lost; it falls to the earth without reaching the stigma, or it is damaged by moisture. All the plants of this category obviate this inconvenience by producing enormous quantities of pollen (*e. g.* the positive clouds of yellow powder which frequently surround the Conifers at the moment of flowering).

But in still more numerous cases the pollen must be conveyed to the stigma by insects; and from this flows a multitude of consequences which greatly influence the form and appearance of the flowers. Thus the perianth will always be more or less coloured or odoriferous, to attract insects; the grains of pollen are not dry and free as in the previous cases, but always more or less adherent to each other, being retained by a product of the degenerescence of the mother cell, which M. Kerner regards (wrongly we think) as *bassorine*. The degree of cohesion is extremely variable, from the solid pollen-masses of the Orchideæ and Asclepiadeæ to the pollen of a great number of plants which presents little conglomerations easily dispersed.

In these plants the pollen is produced in quantities infinitely smaller than in the anemophilous plants. Moreover there is a more or less considerable lapse of time between the opening of the anthers and the moment when the fecundating dust is carried away by insects; and it is absolutely necessary that during this time it should be protected from the deleterious influences of wind and moisture. The most various parts of the flower may be charged with this function; and it is the examination of the different cases which he has had the opportunity of observing that forms the greater part of M. Kerner's memoir.

The reproductive organs themselves are often charged with the protection of the pollen. Thus, in the iris the stigmata are developed into broad petaloid plates bent outwards and meeting the lobes of the perigonium; they thus completely envelope the anthers in a sort of narrow channel, through which insects must of necessity pass when going to collect the nectar, but into which neither wind nor rain can penetrate. In the genus *Aspidistra* the corolla takes on the form of a widely open cup, at the bottom of which are the extremely short stamens; the stigma is developed into a broad disk,

placed about halfway up the corolla and closing it completely, so as to shelter the stamens and leave only a narrow passage for insects. In the periwinkles, oleanders, &c. the anthers bear at their summits a sort of spoon-shaped prolongation, and the style is surrounded by a collar of long stiff hairs; the junction of these two organs forms a perfect roof above the pollen. In the Compositæ the tube formed by the union of the anthers, in the interior of which is the pollen, shelters it until the moment when insects come to collect it.

Frequently the protective shelter comes from the *perianth*. A great number of plants have a portion of the corolla developed into the form of a regular roof placed over the anthers. This peculiarity of organization is characteristic of some very important families (such as the Labiatæ, Scrophulariaceæ, Orobancheæ, Gesneriaceæ, Utriculariæ, Polygaleæ, Violaceæ, many Papilionaceæ, and some Ranunculaceæ).

In other cases the upper part of the lobes of the corolla remains united during the first portion of the flowering, thus protecting the stamens and the style (*Phyteuma*); or, as in *Trollius*, the petals, which are strongly concave within, join at the top of the flower. In other cases, again, the tube of the corolla which encloses the anthers is so narrow that water cannot penetrate into it, the air finding no means of exit and remaining enclosed in the form of a bubble, which keeps the pollen dry (*Androsace*, *Verbena*); or, what is still more frequent, the entrance of the tube is closed by hairs, scales, &c.

The *spathe* in many Aroïdeæ, the *bracts* of certain Musaceæ, and the *leaves* of the lime tree extend over the flower or the inflorescence like an umbrella.

When no part of the flower is constructed so as to be able to shelter the stamens from the weather, the desired result is obtained either by periodical movements of the perianth or by curvatures of the axis.

In the first category we find, in the first place, all the so-called ephemeral flowers, the opening of which lasts only one day (*Villarsia*, *Tradescantia*, *Convolvulus tricolor*, *Tigridia pavonia*, and many others). The anthers open and allow the pollen to escape in the bud, which on its part opens only during the hottest part of the day, when the sun is shining, and the insects, buzzing about everywhere, are ready to effect fecundation. Those flowers which present a similar structure, but of which the anthesis lasts several days, are governed by similar laws; they close during the cooler hours, when the dew might injure the pollen, and also during rainy weather and when little life is about. Some of them particularly affect twilight and evening; they only open a little after the setting

of the sun, and close in the course of the evening. Their usual visitors are of course the crepuscular insects; and to attract these some are clothed in brilliant colours (nightshade and several *Œnotheræ*), whilst others have very dull colours but exhale a penetrating perfume, which is insensible during the day (*Pelargonium triste*, *Hesperis tristis*, *Nyctanthes arbor-tristis*). But these cases are quite exceptional, and the great majority of flowers with periodical movements open during the brightest hours of the day; the petals, in closing again, resume the position they occupied in the bud, and thus completely protect the stamens and the style.

Where it is by means of curvatures of the floral axis that fecundation is ensured, the perianth must be brought into such a position as to form a protective roof for the reproductive organs. Its form, and also the degree of curvature, depend of course greatly upon the length of the stamens: where, as in the lily of the valley, these are quite short, a slightly developed perianth and a simple lateral inclination suffice to attain the desired object; but where, as in the fuchsia, the anthers are borne upon long filaments, the perianth is much broader and spread out like a wheel, and the flower becomes completely pendent.

All degrees of curvature are met with in nature: sometimes the phenomenon is already perceptible in the bud (*Soldanella*); in other cases it is manifested only at the moment of flowering. When once fecundation is effected the young fruit usually becomes erected, at least if it is not of a fleshy nature, and consequently too heavy to be carried up by the tension of the tissues of the peduncle (*Fuchsia*, many *Solana*).

It is sometimes the case that the curvature of the axis, like the closing of the perianth, is periodical. Thus the flower of *Oxalis acetosella*, which is completely erect during the day, describes an arc of more than 100 degrees at the moment when the sun sets, and finally has its opening directed towards the ground. The periodical changes in the tension of the tissues of the peduncle required by this movement occur in many other plants under the influence of exterior excitements, repeated shocks, &c.; and many flowers which are usually erect become recurved towards the earth, and thus protect their stamens when they are shaken by the wind or disturbed by the repeated shocks of drops of rain (many Compositæ, tulips, anemones, *Ranunculus*, poppies).

Lastly, in those compound inflorescences of which the axis is twisted, as in the Borragineæ and some other families, development brings the flowers successively into all sorts of

positions with regard to the horizon; they then most frequently open in such a manner that at the moment when the pollen would be exposed to inclement weather the opening of the corolla looks towards the ground, and thus the rain may pour upon them without injury.

Such are the different peculiarities of organization, the special object of which is to facilitate fecundation by protecting the pollen from accidents which might injure it, without, however, presenting any obstacle to the free access of insects whose business it is to cooperate in the accomplishment of that function. Of course these different means are often combined: for example, if a flower in closing at night leaves an aperture at the apex of the corolla, it will be borne upon a more or less curved peduncle.

In a general way we may say that the pollen is more completely protected in proportion as it is less abundant and more coherent, and in proportion as the fecundation is more absolutely subjected to the intervention of insects, the time of anthesis short, and the climate less favourable.

Thus the Orchideæ perhaps present the most complete combination of all the means of protection, which is in perfect accordance with the nature of their pollen and the small number of their flowers. In the Pomaceæ and Amygdaleæ, on the other hand, the stamens are very numerous, and the flowers are so abundant that if only half of them developed fruit the tree could never bear its load. Hence the means of protection employed are very rudimentary.

Even a superficial glance over the flora of a country will generally show an intimate relation between the climatal conditions and the structure of the most wide-spread families. A cold and humid region (where fecundation will always be difficult and where the flowers must sometimes wait for several days for a ray of the sun to favour the issue of insects) cannot fail to exert a marked influence upon the character of its flora. It is thus that in the Alps, where the dews are very heavy and where persistent clouds often cover the summits for whole days, the dominant genera (*Gentiana*, *Primula*, *Andromeda*, *Soldanella*, *Pedicularis*, *Campanula*, *Euphrasia*, *Veronica*, &c.) all possess complete means of sheltering their pollen. No plants with ephemeral flowers occur there; and in none do the stamens rise much above the corolla. If, on the other hand, we take as a point of comparison the flora of the south of Australia, a region where during the season when plants flower not a drop of water falls, we find that the *Mimoseæ*, *Myrtaceæ*, and *Proteaceæ* (which are so abundant there) all have rigid flowers with very

short perianths and very long stamens—in a word, flowers in which the pollen is completely exposed.

Some plants which seem at the first glance to form an exception to the general rules above laid down, when attentively examined really serve to confirm them. The *Ericæ*, for example, present the anomalous combination of a pulverulent pollen with a coloured perianth producing nectar. But here, just as in plants with coherent pollen, fecundation is impossible without the intervention of insects. In fact the anthers only open by two pores placed laterally at the apex of each cell; at the moment of flowering they are applied to each other by their lateral surfaces so as to close all issue for the pollen. To enable the latter to issue it is necessary that an insect entering the flower should produce a shock upon one stamen, which separates from its neighbours, lets fall a few grains of pollen upon the visitor, and then resumes its place. Some little appendages which are developed at the base of the anthers, and bar the passage of the insect, are exactly destined to produce the required movement.

Analogous peculiarities occur in some Boragineæ of the genera *Cerinthe* and *Onosma*.

Certain *Salices*, of which the pollen, although more or less coherent, is not at all protected, remedy this by producing an enormous quantity of pollen, and by prolonging their flowering for a very long time (a circumstance which recurs with the same signification in many Umbelliferæ, Cruciferæ, and Saxifragaceæ). Sometimes, also, parts of the inflorescence which are already withered become a protection for those which are about to open.

We may remark also among heterostylous plants, such as the *Primulæ*, *Pulmonariæ*, &c., a marked tendency to dimorphism of the perianth. It is more amply developed in the form with long exserted anthers, where the protection of the pollen is more difficult.

M. Kerner concludes his interesting memoir by some considerations on the probable origin of the species with coherent pollen, in which we shall not follow him: they do not appear to us to be necessarily connected with the preceding; and the ideas of the author merit a discussion of which space will not permit the introduction here. These pages suffice to show the object and utility of the infinite variety of form of the floral organs.